



NOTES ON THE DISTRIBUTION OF *BRASENIA SCHREBERI* (CABOMBACEAE) IN THE NEOTROPICS, WITH A NEW COUNTRY RECORD FOR COSTA RICA

Rafael Acuña-Castillo^{1,2} , José E. Jiménez^{2,3} , Luiz E. Bezerra-Silva⁴ ,
Jorge San Gil-León¹  & Mario A. Blanco^{1,2} 

¹ Escuela de Biología, Universidad de Costa Rica, Apdo. 11501-2060, San José, Costa Rica; rafael.acuna_cast@ucr.ac.cr (author for correspondence).

² Herbario Luis A. Fournier Origgí, Centro de Investigación en Biodiversidad y Ecología Tropical (CIBET), Universidad de Costa Rica, Apdo. 11501-2060, San José, Costa Rica.

³ Gestión de Grupos Turísticos e Ingeniería en Ciencias Forestales y Vida Silvestre, Universidad Técnica Nacional, Apdo. 1902-4050, Alajuela, Costa Rica.

⁴ Programa de Posgrado en Biología, Universidad de Costa Rica, Apdo. 11501-2060, San José, Costa Rica.

Abstract. Acuña-Castillo, R., J. E. Jiménez, L. E. Bezerra-Silva., J. San Gil-León & M. A. Blanco. 2021. Notes on the distribution of *Brasenia schreberi* (Cabombaceae) in the Neotropics, with a new country record for Costa Rica. *Darwiniana*, nueva serie 9(2): 364-374.

We studied herbarium specimens of *Brasenia schreberi* from the Neotropics in order to describe the distribution pattern of the species across the region. Also, we report the first records of *B. schreberi* for Costa Rica. We confirm that *B. schreberi* has a sporadic pattern of distribution in the region and also in most neotropical countries where it has been collected. For this reason and because of its apparent disappearance from some localities, we recommend *B. schreberi* to be considered Vulnerable in the Neotropics.

Keywords. Aquatic plants; floristics; geographic distribution; Neotropics; Nymphaeales; threatened species.

Resumen. Acuña-Castillo, R., J. E. Jiménez, L. E. Bezerra-Silva., J. San Gil-León & M. A. Blanco. 2021. Notas sobre la distribución de *Brasenia schreberi* (Cabombaceae) en el Neotrópico, con un nuevo registro para Costa Rica. *Darwiniana*, nueva serie 9(2): 364-374.

Estudiamos especímenes de herbario de *Brasenia schreberi* recolectados en el Neotrópico para describir el patrón de distribución de la especie en la región. Además, registramos aquí por primera vez la presencia de *B. schreberi* en Costa Rica. Podemos confirmar que *B. schreberi* tiene un patrón de distribución esporádico en la región y también en la mayoría de los países neotropicales donde se ha recolectado. Por esta razón, y por su aparente desaparición de algunas localidades, recomendamos que *B. schreberi* se considere como Vulnerable en el Neotrópico.

Palabras clave. Distribución geográfica; especie amenazada; florística; Neotrópico; Nymphaeales; plantas acuáticas.

INTRODUCTION

It is widely accepted that, with the exception of *Amborella trichopoda* Baill. (Amborellaceae), the order Nymphaeales is sister to all the remaining extant angiosperms, based on phylogenetic

evidence from both plastid and nuclear DNA sequence data (Li et al., 2019; Yang et al., 2020; Zhang et al., 2020). Although not particularly species-rich (94 spp: Barbosa et al., 2018; Govaerts, 2021; Lima et al., 2021), Nymphaeales has a subcosmopolitan distribution, being widespread

in lentic, or rarely lotic, freshwater habitats of all continents and regions, except the polar ones and, with few exceptions, most deserts and mountainous regions (Stevens, 2001; La-onsri et al., 2009; Christenhusz et al., 2017). Of the three families of the order, morphologically aberrant Hydatellaceae (13 species: Govaërts, 2021) is restricted to India, Australia and New Zealand (Sokoloff et al., 2019). Nymphaeaceae, with 75 spp, is found in all continents except Antarctica, and its distribution basically corresponds to that of the order (Lima et al., 2021). Finally, Cabombaceae is native to all continents, except Antarctica and Europe, but outside the Americas its distribution seems to be restricted and localized. It only has seven accepted species (Ørgaard, 1991; Wiersema, 1997; Barbosa et al., 2018) in two genera: *Cabomba* Aubl. (6 species) and *Brasenia* Schreb. (1 species) are extant. The first genus is native to the lowlands of tropical and warm temperate regions of the Americas, from Ontario, Canada, to Río Negro, Argentina (Wiersema, 1997; Ospina & Zanotti, 2015), but *C. caroliniana* A. Gray has been introduced to and is considered an invasive species in other continents (particularly Asia, Australia, and Europe; CABI, 2020). *Brasenia schreberi* J.F. Gmel. on the other hand, has extant native populations on all continents except Europe (although there is fossil evidence of its presence there in the recent geologic past; Drzymulska, 2018) and Antarctica (Verdcourt, 1971; Cook et al., 1974; Wiersema, 1997; Fu & Wiersema, 2001; Stanley & Orchard, 2007). In the Americas this species has been reported from as far north as Alaska and Newfoundland (with populations on eastern and western North America separated by the Rocky Mountains and the Great Plains, Wiersema, 1997) to as far south as NW Venezuela and Guyana (Goebel, 1893; Wiersema in Hokche et al., 2008). In this paper we review the distribution of *B. schreberi* across the Neotropics and report its occurrence in Costa Rica for the first time.

MATERIALS AND METHODS

Collections examined. Examination of specimens of *Brasenia* that were collected in the Neotropics was conducted in the online

catalogues of COL, F, MA, MO, K, NY, P, U, US, USF and VT (herbaria acronyms as per Thiers, 2021). Additional specimen images were kindly provided by the staffs of EAP, LAGU, TEFH, PSO and the herbarium of the Corporación Autónoma Regional para la Defensa de la Meseta de Bucaramanga (CDMB, not in Index Herbariorum). Additional records were obtained from the iNaturalist platform and the literature. We mapped the examined specimens (and unequivocal photos) using the R-package maps (Becker & Wilks, 2018). The collection localities were retrieved from the specimen labels. When no coordinates were given, we estimated the collection locality as precisely as we could, using the geonames.org website, or Google Earth.

Field work. Field work was carried out in the Cureña district of Sarapiquí county, Heredia province, Costa Rica, in the lagoon systems of La Marina, Copalchí and Tambor, within the limits of the Refugio Nacional de Vida Silvestre Mixto Maquenque (RNVSM) in the Area de Conservación Huetar Norte. The Copalchí lagoon has an approximate area of 136660 m² (Clima Pesca, 2017) and according to the Instituto Meteorológico Nacional de Costa Rica, the average atmospheric humidity in the area is 88.5%, with 3525 mm of average yearly precipitation and an average temperature of 26.6 °C. The RNVSM is located at low elevations with the Copalchí lagoon at approximately 23 m a.s.l. The wetland vegetation is dominated by several Poaceae species, as well as *Ludwigia* L. sp. (Onagraceae) and *Nymphaea* sp. The lagoon has a maximum depth of about 2 m and the presence of the large tropical gar (*Atractosteus tropicus* Gill, 1863) has been noted by us. Representative specimens of *Brasenia schreberi* collected in the region are deposited in USJ (Thiers, 2021).

RESULTS AND DISCUSSION

Brasenia Schreb., Gen. Pl., ed. 8[a]. 1: 372. 1789.
Type species. *Brasenia schreberi* J. F. Gmel.

Hydropeltis Michx., Fl. Bor.-Amer. (Michaux) 1: 323. 1803. Type species. *Hydropeltis purpurea* Michx.

Brasenia schreberi J. F. Gmel., Syst. Nat., ed. 13[bis]. 2(1): 853. 1791. TYPE: United States, New Jersey:[WarrenCo.], Hope[Township?], s.d., *Floyd 1* (holotype: M 0110828!).

Hydropeltis purpurea Michx., Fl. Bor.-Amer. (Michaux) 1: 324, t. 29. 1803. *Brasenia peltata* Pursh, Fl. Amer. Sept. (Pursh) 2: 389. 1813. Nom. superfl. *Brasenia nymphoides* Baill., Hist. Pl. (Baillon) 3: 82, footnote. 1871. Nom. superfl. *Brasenia purpurea* (Michx.) Casp., Journ. Sci. Math. Phys. Nat. 4(16): 312. 1873. *Cabomba peltata* (Pursh) F. Muell., Fragm. (Mueller) 10(85): 77. 1876. Nom. superfl. Probable original material: [United States:] In Aquis Carolinae, s.d., *A. Michaux s.n.* (P 00752297!); Amer. Sept., s.d., *A. Michaux s.n.* (P 00752298!); sine loc., s.d., *A. Michaux s.n.* (P 00675228!).

Hydropeltis pulla Salisb., Ann. Bot. [König & Sims]. 2(1): 74. 1805. TYPE: Canada, 1800, *F. Masson s.n.* (BM 000574916, not seen).

Brasenia hydropeltis Muhl., Cat. Pl. Amer. Sept.: 55. 1813. Probable original material: United States, Pennsylvania, Lancaster, 1799, *H. Muhlenberg 671* (LINN hs925-1!); *H. Muhlenberg [?] 795* (PH 00034888!).

Plants of *Brasenia schreberi* grow submersed and have been described as “free-floating” but are often fixed to the bottom by their adventitious roots that emerge from the stem nodes and have well-developed root caps that act as anchors (Arber 1920). They produce “trailing” stems (Fig. 1) that can reach 3 m or more in length and creep on the surface of the mud. Leaves are alternate (occasionally appearing opposite by production of leaves from short, axillary branches) with petioles up to 80 cm long. The leaf blades are oval, entire, centrally peltate and floating (Fig. 1A), 6-12 cm long and 4-6 cm wide (Williamson & Schneider, 1993), with the adaxial surface bright green and the abaxial surface purple. All submersed parts are usually thickly coated with a clear mucilage (Fig. 1E), which is secreted by glandular trichomes. Flowers are solitary and produced from the axils of leaves on long purplish pedicels (Raciborski, 1894; Arber, 1920; Wood, 1959). In areas with cold winters, the tips of the stems develop turions that sink to the bottom, supposedly to resist the winter (but Adams [1969] found no evidence of their

survival over the winter); it is unknown if similar turions are produced in tropical habitats.

The flowers of *Brasenia schreberi* are protogynous, to ca. 2 cm in diameter (Osborn & Schneider, 1988) with the perianth, androecium and gynoecium dark purple (Fig. 1C). The perianth is composed of six to eight purple tepals, 1-2 cm long, 0.5 cm wide (Rahayu & Magandhi, 2018) organized in two whorls. The androecium has ca. 18-36 stamens (also in two whorls; 18-51 reported by Les, 2004) and the anthers are ca. 4 mm long (Williamson & Schneider, 1993). The gynoecium has six free carpels with two ovules in each (Raciborski, 1894; Wood, 1959; but 4-18 carpels reported by Les, 2004). Anthesis is diurnal, with individual flowers emerging from the water and opening in the morning and closing and going back into the water in the afternoon, for two consecutive days (dianthesis). First-day flowers have short, undehisced stamens and elongated, papillate stigmas; second-day flowers have elongated staminal filaments with dehisced anthers. Pollination is by wind (Osborn & Schneider, 1988). Little is known about the mechanism of seed dispersal, but Hill (1900) observed that the peduncles (pedicels?) bearing fruits apparently separate and float away from the mother plant.

Nomenclatural notes. Sometimes “Rondachine” (Bosc, Encyclopédie méthodique. Agriculture. 6: 180. 1816) is considered a synonym of *Brasenia*, however to us it appears that it is merely a common name intended for *Brasenia*. *Brasenia nymphoides* has been considered to be another combination of *Menyanthes nymphoides* L. (footnote 3 in Baillon, Hist. Pl. 3: 82. 1871), however we consider this a misapplication of the name that probably stemmed from the usage of *Limnanthemum peltatum* Griseb., (in Gen. Sp. Gent. 348. 1838. non S. G. Gmel. Novi Comment. Acad. Sci. Imp. Petrop. 14(1): 527 (t. 17). 1770), as Grisebach included in it Thunberg’s concept of *Menyanthes nymphoides*, which is not that of Linnaeus: e.g. specimens labeled *Limnanthemum peltatum* Griseb. in L (L 1708423!) and P (P 01956399!) are *Brasenia schreberi*. We consider *Brasenia hydropeltis* as heterotypic to *Hydropeltis purpurea*: Muhlenberg (1813) did not cite Michaux or his specimens, instead citing the habitat of *Brasenia hydropeltis* as “Pens.” [Pennsylvania].

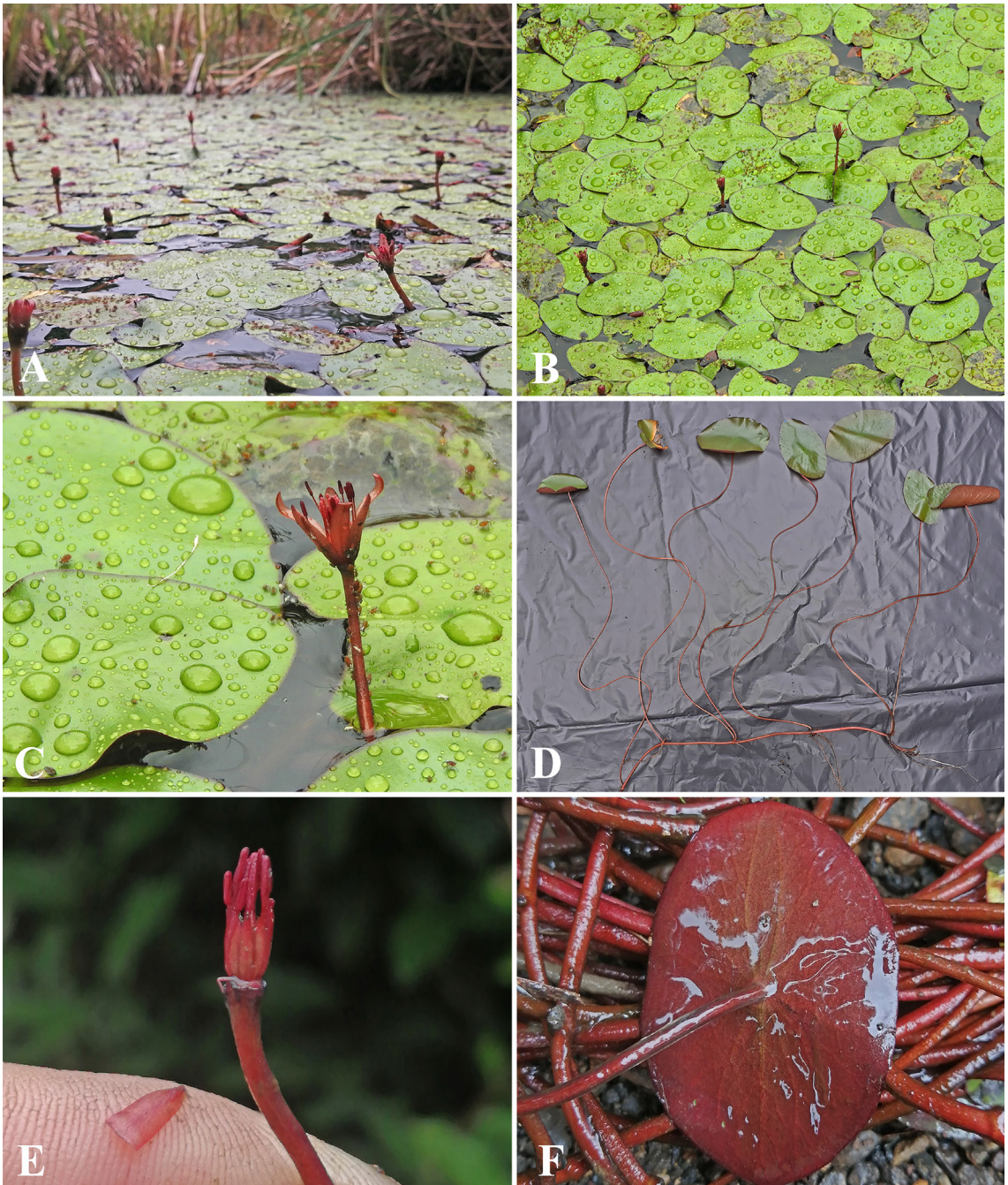


Fig. 1. *Brasenia schreberi*, from RNVSM, Heredia province, Costa Rica, *Acuña et al.* 2217 and *Jiménez et al.* 5437 (both USJ). **A**, habitat, in a small, tropical, lowland lagoon. **B**, floating, peltate leaves and anthetic flowers. **C**, anthetic flower, with aphids on the pedicel and on the adaxial surface of some leaves. **D**, habit, notice the elongated petioles and the trailing stem. **E**, flower with tepals removed, showing androecium (partial) and gynoecium (complete). **F**, underside of a floating leaf covered in mucilage. Color version at <http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/988/1235>

Economic importance. *Brasenia schreberi* has culinary importance, it is cultivated and widely consumed in China, Japan and Korea, and the roots eaten by Native Americans (Les, 2004, 2018). It has traditional medicine importance due to the high content of antioxidants in the form of polysaccharides (Xiao et al., 2016). The mucilage also has allelopathic properties (Elakovich & Wooten, 1987) and may reduce herbivory on the species (Thompson et al., 2014). The species also has been used as a decorative plant in aquaria and water gardens and is considered a pest in Missouri (Les, 2004, 2018).

Ecology. *Brasenia schreberi* often grows in acidic water bodies (Les, 2004; Kim et al., 2008, 2012) but could tolerate alkaline conditions as well (Les, 2018). It prefers shallow water to a depth of up to 3 meters, in areas fully exposed to the sun. Under good environmental conditions, *B. schreberi* can cover water bodies quickly, since new shoots form easily from its trailing stems (Rahayu & Magandhi, 2018). Its tolerance to water turbidity and its allelopathic interactions could contribute to its dominance in some localities (Les, 2018). Carps (Cyprinidae), turtles (Testudines), waterfowl (Anatidae), moose (*Alces alces*, Cervidae), aphids (Hemiptera), beetles (Coleoptera) and moths (Lepidoptera) are known to consume this species (Ernst & Lovich, 2009; Les, 2018; Rahayu & Magandhi, 2018).

Distribution in the Neotropical Region (Fig. 2)

WEST INDIES: The species seems to be restricted to lakes, lagoons, and ponds in the lowlands of Cuba, Jamaica, and the Dominican Republic. Judging by the number of specimens examined, it appears that the species could be more common in the western part of Cuba than elsewhere in the Neotropics.

MEXICO: *Brasenia* can be found both in lowland and mid-elevation localities. It seems mostly restricted to the south of the Tropic of Cancer (Jalisco, Michoacán, San Luis Potosí, Veracruz, Tabasco, and Chiapas: Villaseñor, 2016; Zepeda-Gómez, 2017), but there is at least one extratropical record from Chihuahua (Lot et al., 2002).

NORTHERN CENTRAL AMERICA: The specimens from the Atlantic slope (Belize, northern Guatemala, and eastern Honduras) were all collected in lowland lagoons, while in those from the Pacific slope (southeastern Guatemala, western El Salvador, and central Honduras: Rivera, 2014) were found in middle elevation lagoons in mountainous areas.

SOUTHERN CENTRAL AMERICA: We record the presence of *Brasenia schreberi* for the first time in Costa Rica. We found the species growing in two sites within the RNVSM of which one was sampled. The sampled plants were found growing on the eastern end of a small lagoon surrounded by forest patches, on the side of a dirt road. The area where *Brasenia* grew had dark, organic material-rich water, 80-100 cm deep. The substrate was muddy and soft, and probably with low oxygen levels, judging by the amount of gases liberated when the plants were collected. A man-made canal, probably to prevent the lagoon to overflow the dirt road, ran under the road allowing some water flow. Associated species include *Annona glabra* L., *Blechnum serrulatum* Rich., *Eleocharis retroflexa* (Poir.) Urb., *Nymphaea* sp., *Rhynchospora corymbosa* (L.) Britton, and *Urospatha grandis* Schott.

The aerial portions of stems (e.g., the flower pedicels) of plants in the wild were infested by aphids (Aphidoidea, Hemiptera). The submerged parts of the plants were heavily coated in a thick layer of mucilage, but a few plants that were collected alive, and transplanted to cultivation, have produced only small quantities of mucus 6 months after transplantation, while staying apparently healthy, producing new leaves, vegetative buds, and stolons.

Brasenia schreberi has not been previously documented in Costa Rica, even in some intensely-collected wetland localities such as Palo Verde, Caño Negro and Tortuguero. This underscores that, to effectively document the wetland flora of the country, more effort has to be invested in lesser known localities. Strangely, *Brasenia* was not mentioned in the recent treatment of Cabombaceae of Costa Rica by Crow (2020), albeit the species was already known from countries both north and south of Costa Rica. Although, as far as we know *Brasenia schreberi* has not been collected

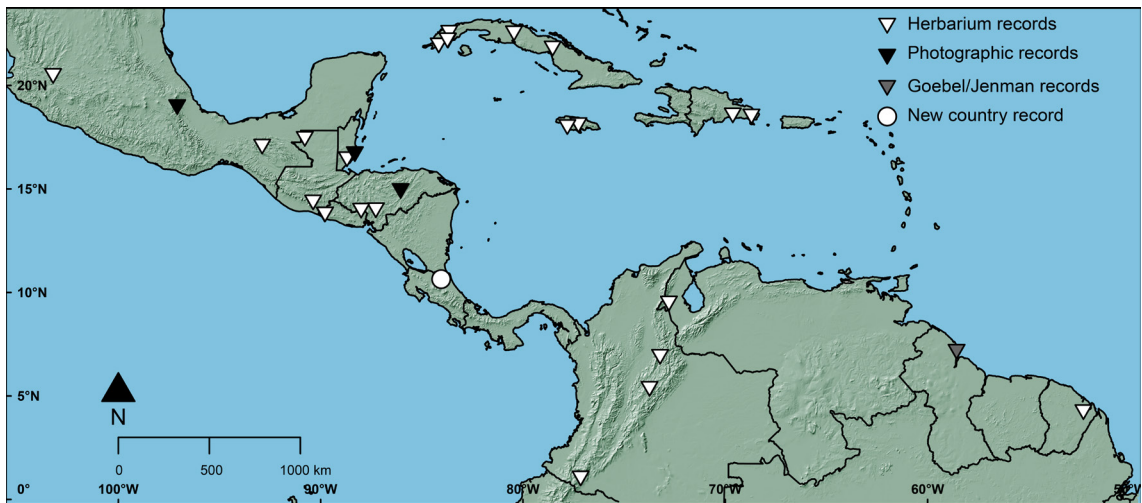


Fig. 2. Distribution of *Brasenia schreberi* in the Neotropics based on herbarium specimens examined in this study, trustworthy reports in the literature (Goebel/Jenman records), and/or unequivocal photographic records (iNaturalist and tropicos.org databases, see text for details). Color version at <http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/988/1235>

in Nicaragua, it is very likely it will be found there, as RNVSM is adjacent to the Nicaraguan border (and the species has been collected at least three times in Honduras).

COLOMBIA: We were able to examine specimens that confirm the unequivocal presence of *Brasenia schreberi* in Colombia, as Camargo (1969) and Schmidt-Mumm (1998) previously reported. However, the species is not cited in the recent Catálogo de las plantas y líquenes de Colombia (Bernal, 2015) and Schmidt-Mumm (1998) considered it as extinct in the Sabana de Bogotá region. Material collected more recently also indicates the species is more widespread in the country than previously thought, and very likely still persists in Colombia. Unlike the specimens of the West Indies, the Caribbean slope of Central America or the Guianas, which were all collected from the lowlands, those from Colombia grew in swamps and lagoons at intermediate or even high elevations in the Andes themselves (ca. 1250–2770 m a.s.l.). Although the species was collected as far back as the late 18th or early 19th centuries in Colombia by José Celestino Mutis and there are confirmed records from at least three Departments, only a handful of specimens have been deposited in herbaria, underlining its potentially very localized distribution in the country.

VENEZUELA: The first records of *Brasenia* in the country were published by Aristeguieta & Agostini (1965) for the states of Mérida and Táchira. Wiersema (in Hokche et al., 2008), also mentions its presence in Zulia (we examined a specimen from western Zulia) and Trujillo. Thus, the species seems to be restricted to the northwestern part of the country. According to the map 14 in Velásquez (1994, p. 114), it could be mostly, or even entirely, restricted to the Maracaibo Lake Basin.

THE GUIANAS: The description and illustrations in Goebel (1893: p. 232 and Tab. XXXI) can be unequivocally assigned to *Brasenia schreberi*. This is one of the few records from Guyana we were able to find in the literature (“*Ich war aber, als ich Brasenia im Tapacooma-See in Britisch Guyana sammelte, doch überrascht, zu sehen, von welcher dicker Lage von Gallerte die sämtlichen jungen Teile überzogen waren.*”). However, it is uncertain if Goebel’s collection was deposited in any herbarium and the specimen, if any, has not been located (A. Fleischmann & H-J. Esser in M, pers. comm. 2021). Cramer (1979) cites that [George Samuel] Jenman collected the species in 1886, also in the Tapakuma lake, but we have not been able to locate his collections either. According to J. Wiersema (US), the species could be extirpated in the country (pers. comm. 2021).

We also examined a single French Guianan collection (several duplicates). Judging from satellite images near the inferred collection locality, it seems like the collection comes from a deeply forested lowland area, as the portion of the RN2 road from Correze and Coralie to Regina seems to be surrounded by dense lowland humid forests. These few records indicate that the species could be rare and found very sporadically in lowland lakes or lagoons surrounded by forests. Cramer (1979) indicates that the species has not been collected in Suriname.

Examined material

BELIZE. **Stann Creek:** Sanctuary Belize, 25-VIII-2003, Jan Meerman available in <https://www.inaturalist.org/observations/32145301> (iNaturalist). **Toledo:** Lowland broadleaved forest. BFREE [Belize Foundation for Research and Environmental Education] Reserve, Lagoon, 45-75 m a.s.l., 15-X-2005, *Whitefoord & Quiroz 106118* (MO); BFREE, 4-II-2008, Jan Meerman available in <https://www.inaturalist.org/observations/32145301> (iNaturalist).

COLOMBIA. **Without locality:** 1783-1808, *Mutis 737* (MA, US). **Cundinamarca:** [Prov. Ubaté], Pantanos Fúquene, 2600 [2540] m a.s.l., III.1930, *Pérez Arbeláez 87* (COL, US). **Nariño:** Prov. Pasto, Corregimiento El Encano, Laguna de La Cocha, total de la Isla Corota. 2770 m a.s.l., 30-IX-2005, *Benavides et al. 57* (PSO). **Santander:** [Prov. Metropolitana], Munic. Girón, Humedal El Pantano, 1282 m a.s.l., 16-V-2013, *Anaya & Herrera 5* (CDMB), same locality and date, *Anaya & Herrera 8* (CDMB).

COSTA RICA. **Heredia:** Cantón Sarapiquí, Cureña: Refugio Nacional de Vida Silvestre Mixto Maquenque, pequeña laguna rodeada de fragmentos boscosos, a orilla del camino a aprox. 700 m al NW del Bar Finca La Alejandra hacia Lagunas La Marina, 40 m a.s.l., 26-I-2021, *Acuña et al. 2217* (USJ), same locality and date, *Jiménez et al. 5437* (USJ).

CUBA. **Without locality.** 1860-1864, *Wright 1859* (K, MO, NY, P, US). **[Ciego de Ávila?]:** Herradura, 28-X-1905, *Cook 134* (US). **Pinar del Río:** Laguna en el camino a Ceja Ana de Luna, Viñales, 11-XI-1989, *Urquiola et al. 5581* (NY); Laguna Jovero and vicinity, 5-7-XII-1911,

Shafer 10826 (NY, US); Laguna Jovero, Remates de Guane, 5-I-1932, *León 15368* (NY); Laguna Santa María, 8-IX-1910, *Britton et al. 7151* (NY); La Máquina, 4-III-1943, *Marie-Victorin 58220* (US, USF). **Villa Clara:** Mordazo, Laguna Pozo Grande, 9-VIII-1923, *Ekman 17028* (NY).

DOMINICAN REPUBLIC. **La Altagracia:** Llano Costero, Laguna la Canasta, 14-IV-1929, *Ekman 12170* (MO, U, US). **[Monte Plata?]:** Savannah land and lake area between Bayaguana and Guerra, 8-XI-1946, *Howard & Howard 9938* (NY, P, US).

EL SALVADOR. **Ahuachapán:** Munic. Apaneca, Lagunita Las Ninfas, ca. 1830 m a.s.l., 28-I-1951, *Fasset 28702* (MO, US); same locality, 26-XII-1998, *Herrera 3794/JBL03794* (LAGU); Laguna Verde, 1829 m a.s.l., 28-XII-1998, *Herrera 3835/JBL03835* (LAGU, MO).

FRENCH GUIANA. **Cayenne:** Route RN2 Cayenne-Régina, 31-V-2010, *González 2419* (MO, P, US).

GUATEMALA. **Petén:** Pozos Xan. Laguna perenne rodeada de bosque y cibal, que se inunda en época lluviosa., 50 m a.s.l., 7-VI-1997, *León et al. 160* (MO). **Santa Rosa:** Laguna de Carrizal, ca. 1600 m a.s.l., V-1892, *Heyde & Lux 3062* (MO, US).

HONDURAS. **Francisco Morazán:** Desvío a San Matías, Laguna El Pedregal a 10 Km N de Tegucigalpa, 1500 m a.s.l., 4-III-2010, *House et al. 5398* (TEFH). **La Paz:** Mt. Verde, 18 Km S de Marcala, frecuente en lagunas y quebradas pantanosas, 1800 m a.s.l., 22-V-1986, *Keyser 1451* (EAP). **Olancho:** Gualaco, 700 m a.s.l., 16-III-2013, *Vilchez et al. 570* available in <http://legacy.tropicos.org/Image/100247647> (tropicos.org).

JAMAICA. **Clarendon/Saint Ann:** Mason River district, ca. 3 miles NW of Kellits, 22-I-1966, *Walker 292* (US). **Saint Elizabeth:** Holland, Vicinity of the Bamboo Avenue, Holland estate, ca. 20 m a.s.l., 4-II-1961, *Proctor & Mullings 21965* (NY).

MEXICO. **State unknown:** Vallée de Mexico, 1875, *Schaffner 483* (NY, P). **Chiapas:** Munic. Pueblo Nuevo Solistahuacán, large pond and adjoining marsh on the eastern side of Pueblo Nuevo de Solistahuacán, 1700 m a.s.l., 26-X-1971, *Breedlove 21529* (F, MO). **Jalisco:** Shallow pond near Guadalajara, 26-VI-1889, *Pringle 2920* (VT).

Veracruz: [Munic. Huatusco?], Locality not available, 8-V-2011, César Lezama available in <https://www.inaturalist.org/observations/74328085> (iNaturalist).

VENEZUELA. Zulia: [Munic. Machiques de Perijá?], Entre km. 20-30 al oeste de la carretera Machiques-La Fría, a lo largo de la vía que conduce entre la carretera y el Asentamiento Aricuaisá y el matadero, en bosque de galería y en zona de bosque en transición entre deciduo y siempre-verde., 100-200 m a.s.l., 4-V-1982, *Bunting & Trujillo 11562* (MO).

COMMENTS

Brasenia schreberi has a wide but very patchy distribution in the northern Neotropics. In most countries where it has been recorded, it is known from one or a few isolated localities and by a similarly low number of herbarium records or verifiable observations. This sporadic pattern of distribution appears to be real, particularly in Colombia, Central America and the Guianas, and not an artifact that could be attributed only to the low intensity of collection efforts at national scales. *Brasenia schreberi* has a very distinctive morphology and in the few localities where it is present, it could be common, so it is unlikely that the species would have been overlooked over such vast expanses of its potential range if its distribution was more homogenous. Although both in Africa and globally the species is listed in the category of Least Concern by the IUCN (Gogue, 2010; Maiz-Tome, 2016), and it appears to be relatively common in temperate North America, it is considered threatened in Mexico (Zepeda Gómez, 2017), Australia (Stanley & Orchard, 2007) and Eastern Asia (Kim et al., 2012; Li et al., 2018) and it has been apparently extirpated from Guyana (Wiersema, 2007) and areas of Colombia (Schmidt-Mumm, 1998), Australia (Stanley & Orchard, 2007), China (Li et al., 2018) and South Korea (Kim et al., 2012). Sculthorpe (1967) suggested that the wide but discontinuous, “anomalous” distributions of *B. schreberi* and some other aquatic macrophytes could be the result of extermination from certain areas during the glacial and post-glacial periods.

While it is possible that *Brasenia schreberi* could eventually be found in more localities and in countries like Nicaragua, Panama or Suriname as well as possibly be rediscovered in Guyana, we expect that these potential discoveries would take place in few localities, over relatively small areas and that will reaffirm the localized and scattered distribution pattern of *Brasenia* in the Neotropics as a whole, as we report here. We recommend the species to be considered Vulnerable (VU) under criteria B2ab(iv) (IUCN Standards and Petitions Subcommittee, 2017). Criterion B2 was selected because, using the GEOCAT tool (Bachman et al., 2011) and a reasonable 5 x 5 km grid, we obtained an Area of Occupancy (AOO) of 725 km². Criterion “a” was selected because of its severely fragmented geographic range (influenced by its absence from seemingly appropriate localities). Criterion “b(iv)” was selected because of the decline in the number of locations or subpopulations (as it happened in, e.g., Colombia and Guyana), hinting that the populations of *B. schreberi* are reduced and could be decreasing in the Neotropics.

ACKNOWLEDGEMENTS

This is a contribution from the research project “Guía de las plantas de los humedales de Costa Rica” (C0-255) registered in the Vicerrectoría de Investigación, Universidad de Costa Rica. We appreciate the field assistance provided by Marco Cedeño (USJ) as well as the comments and help offered by John Wiersema (US), Hans Joachim Esser (M) and Andreas Fleischmann (M), when trying to locate the Guyanese material of *Brasenia* collected by Karl Goebel. Mary Merello (MO), Ludy Archila (Corporación Autónoma Regional para la Defensa de la Meseta de Bucaramanga, CDMB), Aida Baca (PSO), Dagoberto Rodríguez (LAGU), Pablo Galán (LAGU), Gabriel Cerén (MHES), Rina Díaz (EAP) and Olvin Hoyuela (TEFH), kindly provided us with access or photographs of specimens from their respective herbaria. We are thankful for the sponsorship from Myrna Stewart and Amanda Bennett, as well as the funding provided by the Vicerrectoría de Investigación, Universidad de Costa Rica, for this project. Two anonymous reviewers made very valuable suggestions that improved the quality of this contribution.

BIBLIOGRAPHY

- Adams, F. S. 1969. Winterbud production and function in *Brasenia schreberi*. *Rhodora* 71: 417-432.
- Arber, A. 1920. *Water plants. A study of aquatic angiosperms*. Cambridge University Press, Cambridge. 436 pp.
- Aristeguieta, L. & G. Agostini. 1965. Un género nuevo para la Flora de Venezuela, *Brasenia* (Cabombaceae). *Boletín de la Sociedad Venezolana de Ciencias Naturales* 26: 140-142.
- Bachman, S.; J. Moat, A. W. Hill, J. de la Torre & B. Scott. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117-126. DOI: <https://doi.org/10.3897/zookeys.150.2109>
- Barbosa, T. D. M.; R. J. Trad, M. M. Bajay, M. I. Zucchi & M. C. E. do Amaral. 2018. Reestablishment of *Cabomba schwartzii* (Cabombaceae), an aquatic plant species endemic to the Brazilian Amazon. *Phytotaxa* 367: 245-255. DOI: <https://doi.org/10.11646/phytotaxa.367.3.4>
- Becker, R. A. & A. R. Wilks. 2018. *maps: Draw Geographical Maps. R package version 3.3.0*. Available at: <https://CRAN.R-project.org/package=maps>
- Bernal, R. 2015 (continuously updated). Cabombaceae. In: Bernal, R., S.R. Gradstein & M. Celis (eds.). *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. Published on the Internet. <http://catalogoplantasdecolombia.unal.edu.co/en/resultados/familia/Cabombaceae/> [April 2021]
- CABI. 2020. *Cabomba caroliniana* (Carolina fanwort). Invasive Species Compendium. Published on the internet: <https://www.cabi.org/isc/datasheet/107743> [April 2021].
- Camargo, L. A. 1969. Nymphaeaceae. *Catálogo Ilustrado de las Plantas de Cundinamarca* 4: 52-53.
- Christenhusz, M. J. M.; M. F. Fay & M. W. Chase. 2017. *Plants of the World: An Illustrated Encyclopedia of Vascular Plants*. Royal Botanic Gardens, Kew, Richmond. 816 pp.
- Clima Pesca. 2017. Laguna Copalchi. Clima Pesca, Países de la Región del SICA. Published on the internet: <https://climapesca.org/2017/08/laguna-copalchi/> [May 2021].
- Cook, C.; B. J. Gut, E. M. Rix, J. Schneller & M. Seitz. 1974. *Water Plants of the World*. Dr. J.W. Junk b.v. Publishers, The Hague. 561 pp.
- Cramer, J. 1979. Cabombaceae. In: A.L. Stoffers & J.C. Lindeman (eds.). *Flora of Suriname, Volume V, Part 1*. E.J. Brill, Leiden: 385-389.
- Crow, G. E. 2020. Cabombaceae. In: B.E. Hammel, M.H. Grayum, C. Herrera & N. Zamora (eds.). *Manual de Plantas de Costa Rica, Volumen IV, Parte 2, Dicotiledóneas (Balanophoraceae-Clethraceae)*. *Monographs in Systematic Botany from the Missouri Botanical Garden* 138: 248-250.
- Drzymulska, D. 2018. On the history of *Brasenia* Schreb. in the European Pleistocene. *Vegetation History and Archaeobotany* 27: 527-534. DOI: <https://doi.org/10.1007/s00334-017-0652-9>
- Elakovich, S. D & J. W. Wooten. 1987. An examination of the phytotoxicity of the water shield, *Brasenia schreberi*. *Journal of Chemical Ecology* 13: 1935-1940. DOI: <https://doi.org/10.1007/BF01014676>
- Ernst, C. H. & J. E. Lovich. 2009. *Turtles of the United States and Canada*. Johns Hopkins University Press, Baltimore. 826 pp.
- Fu, D. Z. & J. H. Wiersma. 2001. Cabombaceae. In: Wu, Z. Y., P. H. Raven & D. Y. Hong (eds.). *Flora of China 6 (Caryophyllaceae through Lardizabalaceae)*: 119-120.
- Ghogue, J. -P. 2010. *Brasenia schreberi*. *The IUCN Red List of Threatened Species* 2010: e.T185681A8457063. [April 2021].
- Goebel, K. 1893. *Pflanzenbiologische Schilderungen. Zweiter Teil. Zweite Lieferung*. N.H. Elwert'sche Verlagsbuchhandlung, Marburg. 386 pp + 31 Tab.
- Govaerts, T. 2021. World Checklist of Hydatellaceae. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; <http://wmsp.science.kew.org/> [April 2021].
- Hill, E. J. 1900. An observation on the water-shield (*Brasenia peltata*). *The Plant World* 3: 153.
- Hokche, O.; P. E. Berry & O. Huber. 2008. *Nuevo Catálogo de la Flora Vascular de Venezuela*. Fundación Instituto Botánico de Venezuela Dr. Tobías Lasser, Caracas. 859 pp.
- IUCN Standards and Petitions Subcommittee. 2017. *Guidelines for using the IUCN Red List categories and criteria. Version 13*. International Union for the Conservation of Nature, Gland, Switzerland. 108 pp.
- Kim, C.; H. R. Na & H. K. Choi. 2008. Conservation genetics of endangered *Brasenia schreberi* based on RAPD and AFLP markers. *Journal of Plant Biology* 51: 260-268. DOI: <https://doi.org/10.1007/BF03036125>
- Kim, C.; J. Jung, H. R. Na, S. W. Kim, W. Li, Y. Kadono, H. Shin & H. K. Choi. 2012. Population genetic structure of the endangered *Brasenia schreberi* in South Korea based on nuclear ribosomal spacer and chloroplast DNA sequences. *Journal of Plant Biology* 55: 81-91. DOI: <https://doi.org/10.1007/s12374-011-9193-4>
- La-onsri W.; C. Trisonthi & H. Balslev. 2009. A synopsis of Thai Nymphaeaceae. *Nordic Journal of Botany*, 27: 97-114.
- Les, D. H. 2004. Cabombaceae. In: Smith, N., S. A. Mori, A. Henderson, D. W. Stevenson & S. V. Heald (eds.). *Flowering Plants of the Neotropics*. Princeton University Press, Princeton: 72-73.

- Les, D. H. 2018. *Aquatic dicotyledons of North America. Ecology, life history and systematics*. CRC Press, Taylor & Francis Group, Boca Raton, London, New York. 1334 pp.
- Li, H.-T.; T.-S. Yi, L.-M. Gao, P.-F. Ma, T. Zhang, J.-B. Yang, M. A. Gitzendanner, P. W. Fritsch, J. Cai, Y. Luo, H. Wang, M. van der Bank, S.-D. Zhang, Q.-F. Wang, J. Wang, Z.-R. Zhang, C.-N. Fu, J. Yang, P. M. Lot. Hollingsworth, M. W. Chase, D. E. Soltis, P. S. Soltis & D.-Z. Li. 2019. Origin of angiosperms and the puzzle of the Jurassic gap. *Nature Plants* 5: 461-470. DOI: <https://doi.org/10.1038/s41477-019-0421-0>
- Li, Z.-Z.; A. W. Gichira, Q.-F. Wang & J.-M. Chen. 2018. Genetic diversity and population structure of the endangered basal angiosperm *Brasenia schreberi* (Cabombaceae) in China. *PeerJ* 6: e5296. DOI: <https://doi.org/10.7717/peerj.5296>
- Lima, C. T.; I. C. Machado & A. M. Giuletta. 2021. Nymphaeaceae do Brasil. *Sitientibus* série Ciências Biológicas 21. DOI: <https://doi.org/10.13102/scb4986>
- Lot, A.; F. Ramos & P. Ramírez-García. 2002. *Brasenia schreberi* J. F. Gmel. (Cabombaceae), un nuevo registro para Chihuahua, México. *Boletín de la Sociedad Botánica de México* 70: 87-88.
- Maiz-Tome, L. 2016. *Brasenia schreberi*. The IUCN Red List of Threatened Species 2016: e.T185681A78457027. DOI: <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T185681A78457027.en> [April 2021]
- Ørgaard, M. 1991. The genus *Cabomba* (Cabombaceae) - a taxonomic study. *Nordic Journal of Botany* 11: 179-203. DOI: <https://doi.org/10.1111/j.1756-1051.1991.tb01819.x>
- Osborn, J. M. & E. L. Schneider. 1988. Morphological studies of the Nymphaeaceae sensu lato. XVI. The floral biology of *Brasenia schreberi*. *Annals of the Missouri Botanical Garden* 75: 778-794. DOI: <https://doi.org/10.2307/2399366>
- Ospina, J. C. & C. A. Zanotti. 2015. Familia Cabombaceae. In: Zuloaga, F. O., M. J. Belgrano & A. M. Anton (eds.). *Flora vascular de la República Argentina* 15: 31-32.
- Raciborski, M. 1894. Die Morphologie der Cabombeen und Nymphaeaceen. *Flora (Jena)* 78: 244-279.
- Rahayu, S. & M. Magandhi. 2018. Teratai jeli (*Brasenia schreberi* J.F. Gmel) di Pulau Samosir. *Warta Kebun Raya* 16: 28-35.
- Rivera, I. 2014. Laguna El Pedregal: Albergue de dos nuevos registros para la flora de Honduras. *Desde el Herbario CICY* 6: 48-51.
- Schmidt-Mumm, U. 1998. Vegetación acuática y palustre de la Sabana de Bogotá y plano del río Ubaté. Tesis de Maestría, Facultad de Biología, Universidad Nacional de Colombia, Bogotá. 195 pp.
- Sculthorpe, C. D. 1967. *The biology of aquatic vascular plants*. Edward Arnold, London. 610 pp.
- Sokoloff, D. D.; I. Marques, T. D. Macfarlane, M. V. Remizowa, V. K. Y. Lam, J. Pellicer, O. Hidalgo, P. J. Rudall & S. W. Graham. 2019. Cryptic species in an ancient flowering-plant lineage (Hydatellaceae, Nymphaeales) revealed by molecular and micromorphological data. *Taxon* 68: 1-19. DOI: <https://doi.org/10.1002/tax.12026>
- Stanley, T. D. & A. E. Orchard. 2007. Cabombaceae. In: Wilson, A. J. G. (ed.). *Flora of Australia Volume 2: Winteraceae to Platanaceae*. Melbourne: ABR/CSIRO Publishing: 275-278.
- Stevens, P. 2001 (continuously updated). Angiosperm Phylogeny Website. Version 14, July 2017. Available at: <http://www.mobot.org/MOBOT/research/APweb/> [April 2021]
- Thiers, B. M. 2021 (continuously updated). *Index Herbariorum, A global directory of public herbaria and associated staff*. New York Botanical Garden, Bronx, New York. Available at: <http://sweetgum.nybg.org/science/ih/>
- Thompson, K. A.; D. M. Sora, K. S. Cross, St. J. M. Germain & K. Cottenie. 2014. Mucilage reduces leaf herbivory in Schreber's watershield, *Brasenia schreberi* JF Gmel. (Cabombaceae). *Botany* 92: 412-416. DOI: <https://doi.org/10.1139/cjb-2013-0296>
- Velásquez J. 1994. *Plantas acuáticas vasculares de Venezuela*. Universidad Central de Venezuela. Caracas. 922 pp.
- Verdcourt, B. 1971. Cabombaceae. In: Turrill W. B. & R. M. Polhill (eds.). *Flora of Tropical East Africa*. A. A. Balkema, Rotterdam: 1-3.
- Villaseñor, J. L. 2016. Checklist of the native vascular plants of Mexico. *Revista Mexicana de Biodiversidad* 87: 559-902. DOI: <https://doi.org/10.1016/j.rmb.2016.06.017>
- Wiersema, J. H. 1997. Cabombaceae. In: Flora of North America Editorial Committee (eds.). 1993+. *Flora of North America North of Mexico. Vol. 3: Magnoliophyta: Magnoliidae and Hamamelidae*. New York and Oxford.: 78-80.
- Wiersema, J. H. 2007. Cabombaceae. In: Funk, V., T. Hollowell, P. E. Berry, C. Kelloff & S. N. Alexander (eds.). Checklist of the Plants of the Guiana Shield (Venezuela: Amazonas, Bolívar, Delta Amacuro; Guyana, Surinam, French Guiana). *Contributions from the United States National Herbarium* 55: 231.
- Williamson, P. S. & E. L. Schneider. 1993. Cabombaceae. In: Kubitzki, K.; J. G. Rohwer & V. Bittrich (eds). *The Families and Genera of Vascular Plants, vol 2. Flowering Plants - Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families*. Springer, Berlin, Heidelberg: 157-161. DOI: https://doi.org/10.1007/978-3-662-02899-5_16

- Wood, C. E. 1959. The genera of the Nymphaeaceae and Ceratophyllaceae in the southeastern United States. *Journal of the Arnold Arboretum* 40: 94-112.
- Xiao, H.; X. Cai, Y. Fan & A. Luo. 2016. Antioxidant activity of water-soluble polysaccharides from *Brasenia schreberi*. *Pharmacognosy Magazine* 12: 193-197. DOI: <https://doi.org/10.4103/0973-1296.186343>
- Yang, L.; D. Su, X. Chang, C. S. P. Foster, L. Sun, C.-H. Huang, X. Zhou, L. Zeng, H. Ma & B. Zhong. 2020. Phylogenomic Insights into Deep Phylogeny of Angiosperms Based on Broad Nuclear Gene Sampling. *Plant Communications* 1: 100027. DOI: <https://doi.org/10.1016/j.xplc.2020.100027>
- Zepeda Gómez, C. 2017. Cabombaceae. In: Lot, A. (ed.). *Plantas acuáticas mexicanas una contribución a la Flora de México. Volumen II Dicotiledóneas Parte I*. Instituto de Biología, Universidad Nacional Autónoma de México, México DF: 41-45.
- Zhang, L.; F. Chen, X. Zhang, Z. Li, Y. Zhao, R. Lohaus, X. Chang, W. Dong, S. Y. W. Ho, X. Liu, A. Song, J. Chen, W. Guo, Z. Wang, Y. Zhuang, H. Wang, X. Chen, J. Hu, Y. Liu, Y. Qin, K. Wang, S. Dong, Y. Liu, S. Zhang, X. Yu, Q. Wu, L. Wang, X. Yan, Y. Jiao, H. Kong, X. Zhou, C. Yu, Y. Chen, F. Li, J. Wang, W. Chen, X. Chen, Q. Jia, C. Zhang, Y. Jiang, W. Zhang, G. Liu, J. Fu, F. Chen, H. Ma, Y. Van de Peer & H. Tang. 2020. The water lily genome and the early evolution of flowering plants. *Nature* 577: 79-84. DOI: <https://doi.org/10.1038/s41586-019-1852-5>